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Preliminary Study on Differentiation of Floral Organs of
Ailanthus altissima (Simaroubaceae)

WANG Yong-Zhou, GU Song[**], REN Yan-Ping, XU Ke, JIANG Sha[**]

(*Nankai University*, *College of Life Science*, Tianjin 300071, China)

Abstract: The investigation of the differentiation and development of inflorescences and flowers in *Ailanthus altissima* (Mill .) Swingle (Simaroubaceae) using light microscopy (LM) and scanning electron microscopy (SEM) suggests: 1) Flower bud differentiation of *A. altissima* occurs in early April on a panicle bearing many flowers; 2) The sequence of floral development proceeds from calyx primordia to corolla primordia to stamen primordia and finally to carpel primordia . Five sepal primordia are initiated spirally and asynchronously . Five petal primordia form nearly simultaneously and grow more slowly than the stamen primordia . The ten stamens are alternately arranged in two whorls; the two whorls develop simultaneously . The 5-carpellate gynoecium grows quickly . 3) In hermaphrodites, the five carpels adhere to each other to form the style and stigma; in staminate flowers, in late developmental stages, the five carpels are sterile and fertile stamens differentiate into anthers and filaments . In this paper, we focus on the morphological transition from bisexual to unisexual flower development in *A. altissima* . We observed that the primordia of staminate flowers are initiated in nearly the same way as in hermaphrodite flowers (although the time of initiation of each organ is different) . The stamen and carpel primordia initiate

simultaneously in both hermaphrodite and staminate flowers . The formation of reproductive structures is due to the differentiation in the course of development of the floral primordia that form the anthers and filaments and or styles, stigmas, and ovaries . The formation of staminate flowers is due to suppression of the development of the gynoecium in *A. altissima* . The mechanism of transition from bisexual to unisexual flowers will only be clarified by further study .

Key words: *Ailanthus altissima*; Floral primordia; Inflorescences; Sex differentiation

Ailanthus altissima (Mill) Swing (*Ailanthus glandulosa* Desf .; Simaroubaceae), a deciduous tree reaching about 20 m in height, occurs in north, east and southwest China . It can withstand drought, tolerates saline and alkaline soils, is fast growing, and is susceptible to few plant diseases and has insect pests . Moreover, the plant is important in afforestation and timber production . Until now, studies on *A. altissima* have mainly focused on its physiological and biochemical properties (Cao, 2004; Gravano *et al* . 1999; Hamerlynck, 2001), drug extraction and identification (Lv and Xiong, 2002; Lv and Liu, 2003) and pollen (Li, 2004) .

Here we wish to report on the development of flowers in *A. altissima* . The differentiation of plant sex is an interesting topic in developmental biology . Generally, there are three types of sex differentiation in flowers: bisexual, unisexual (staminate or pistillate) and nonsexual . These types of flowers appear in many different plant groups and in diverse forms in plant populations . Wyatt (1983) reported that plant sex may be divided into three levels: (1) single flower level, which include three types, hermaphroditic, staminate and pistillate; (2) individual plant level, of which there are seven types, hermaphroditic, monoecy, androecy, gynoecy, andromonoecy, gynomonoecy and trimonoecy; and (3) population level, which includes haploid and multitudinous groups . Dioecy, androdioecy, gynodioecy and trioecy belong to the latter group . Korpelainen (1998) reported that labile sex expression in plants is seen as an ability to modulate sex expression is generally advantageous and can be viewed as adaptation to unstable environments . How sex expression at three levels comes into being in nature is still unclear .

There are various reports on sex expression in plants . For example, sex expression in the cucumber (*Cucumis sativus* L .) is influenced by genotype and plant hormones, such as ethylene (Takahashi *et al* . 1983) . Sex differentiation in *C. sativus* appears to be determined by the selective arresting of the stamen or pistil primordia . When treated with an ethylene-releasing agent or an inhibitor of ethylene biosynthesis at different developmental stages of the flower buds, sex determination is influenced only at the stage of stamen primordia differentiation in both monoecious and gynoecious cucumbers (Yamasaki *et al* . 2003) . In higher plants that bear unisexual flowers, therefore, sex differentiation occurs by the selective arresting of preformed sexual organs in the flower buds during bisexual development (Dellaporta and Calderon-Urrea, 1993) . In most species, for examples in *Silene latifolia* (Grant *et al* . 1994), asparagus (*Asparagus officinalis* L .) (Caporali *et al* . 1994), *Rumex acetosa* L . (Ainsworth *et al* . 1995), *Pistacia vera* L . (Hormaza and Polito, 1996), the flowers are morphologically bisexual during the early stages of development, and ultimately unisexuality results from a secondary unbalanced growth in the androecium and gynoecium . Additionally, sex expression in some plants is related to resource investment (Doust *et al* . 1986) . In unisexual plants, cell death in individual flower buds suppress one or another organ and lead to the abortion of organic primordia during an early stage of sex determination . Cell death may take place during the development of staminate and pistillate organs, and during gamete formation (Wu and Cheung, 2000) .

Plants of *Ailanthus* are polygamous and dioecious (Chen, 1997) . The transition from bisexual to unisexual flowers is still unknown . The great variability in reproductive systems in *Ailanthus* may offer clues in understanding the formation of sexual differentiation . Consequently, we focused on the morphology and structure of sexual transition . Detailed anatomical and morphological observations on floral differentiation in *A. altissima* can supply much more data about reproductive biology, and provide information on the genetic control of sexual determination for future molecular biological studies in these plants .

1   Materials and methods

Plants of *Ailanthus altissima* were grown in an open field on the campus of Nankai University, Tianjin City, China . Individuals of *A. altissima* (tree-of-heaven) with staminate and hermaphroditic flowers was used for all analyses . Inflorescences and buds at various developmental stages were obtained and fixed in FAA (formalin: acetic acid: 50% ethyl alcohol = 5 6 89 v v) . Material for scanning electron microscope (SEM) examination were fixed in 4% (v v) glutaraldehyde in a phosphate buffer, followed by dehydration through an ethyl alcohol series, sputtered with gold and examined by SEM (S-3500N) and photographed .

2   Results

2.1   Morphology and structure of the inflorescence and flower

The inflorescence of *Ailanthus altissima* is an apical panicle on new branches . The flowers are pea green and borne on a pedicel 1 - 2.5 mm long . Five sepals alternate with five petals, which have rigid hairs at the bilateral base . The 10 stamens are arranged in two whorls, the outer five stamens are opposite the petals and the inner five are opposite the sepals . Rigid hairs are at the base of linear filaments . The filaments are longer than the petals in the staminate flowers, but shorter in the hermaphroditic flowers . The anthers are oblong . Five carpels are opposite the petals . In the staminate flowers, the five carpels are degenerate when the flowers are mature, whereas in the hermaphroditic flowers, they develop into an apocarpous gynoecium with a fused style and 5-lobed stigma . The flowering phase lasts from early April to late May .

2.2   Initiation and development of inflorescence primordia

2.2.1   The transition of SAM from vegetative growth to the reproductive growth   Oblong axillary buds occurs in the axils of newly formed branches in early May of the first year . Three or four primordia of compound, alternate leaves are revealed when 2 or 3 scales are removed . The vegetative apical meristem, in the shape of a dome (Plate : 1), is slightly protuberant and laterally elongated . It produces the primordia of compound leaves . During the winter, that scales that cover the apical meristem and young leaves become thicker and harder . In early April of the second year the outer scales become looser, the buds grow to about 1cm long, and the leaves increase in length . The buds grow

rapidly and form new branches . The apex of the new branches elongates and continually produces leaf primordia . The main inflorescence axis arises in the axil of compound leaves . The primordia of the main inflorescence axis are flat (Plate : 2) .

2.2.2   Initiation of the primordia of main inflorescence axes   Shoot apical meristem (SAM) produces the primordia of the compound leaves and inflorescence, which are complex in *Ailanthus altissima* . The primordia of the main inflorescence axis are located in the axils of the primordia of compound leaves and appear oblate . On the two sides of each main inflorescence axis, a pair of bract primordia forms (Plate : 3) . In late April, differentiation of primordia of the main inflorescence axes is completed and SAM differentiates the bract primordia . Three to eight main inflorescence axes are simultaneously arranged at the apex of new branches . The primordia of the lateral inflorescence occur on each main inflorescence axis (Plate : 4) . With the development of inflorescence primordia, the primordia of the compound leaves gradually degenerate .

2.2.3   Initiation of primordia of lateral inflorescence   The primordia of the lateral inflorescences form in the axils of the developing bract primordia (Plate : 5), which form the first branches of the whole inflorescence axes . Later, the primordia of the lateral inflorescence axes develop further . New bracts and lateral inflorescence primordia, which form the secondary branches, are generated from the base of the first branches (Plate : 6) . No additional branches generate on the secondary branches . The floral primordia form on the ends of each secondary branch . The branches of the inflorescence appear as compound raceme-like inflorescences .

The lateral inflorescence are in opposite pairs, but form asynchronously (Plate : 7) . After the transition of the apical meristem from vegetative to reproductive, there are about 15 layers of branches on each main inflorescence axis . The first branches occur from 1 to 6 layers . The secondary branches only occur from 1 to 2 layers . Flowers, which are about 6 to 7 layers of near the top of the main inflorescence axis, are 3 flowerlets in a cluster and alternately arrange . The inflorescence, which is a compound panicle of raceme-like branches
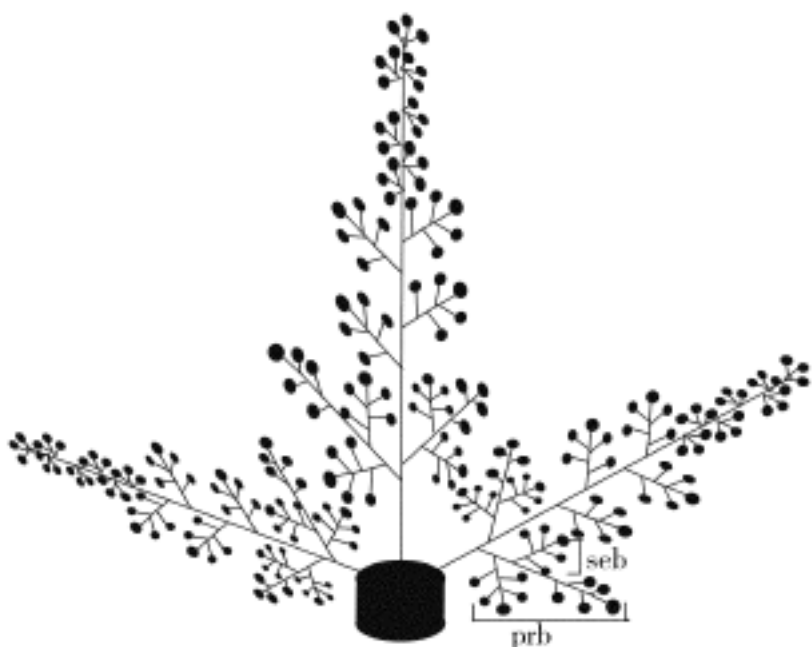
Fig . 1   Diagram of inflorescence of *Ailanthus altissima*
(Mill .) Swingle plant
Prb . first branch; Seb . secondary branch

(Fig . 1) , and the flowers develop acropetally .

2 . 3 Differentiation and development of floral primordia

The floral organs begin to differentiate in late April and finish in late May . The sequence of floral organ differentiation is: calyx primordia, corolla primordia, stamen primordia and pistil primordia .

2.3.1   Differentiation of calyx primordia   The apex of the flower primordium becomes wider and flatter in late April . The sepal primordia, which develop asynchronously and spirally, initiate from the margin of the flower primordium . The first initiated sepal is always situated adaxially in the axil of a bract (Plate   : 8) , the secondary sepal is opposite the first sepal and in an abaxial position, the third is situated opposite the bract (Plate   : 9) , finally, the fourth and fifth primordia differentiate between the first and second and first and third sepal, respectively (Plate   : 10) . The apex of the floral primordium further develops and expands to become flatter due to the activity of the peripheral meristem of the floral primordium (Plate   : 11) .

2.3.2   Differentiation of corolla primordia   In early May, with the development of sepal primordia, the floral primordia become wider and pentagonal in shape . The petal primordia appear inside of and alternate with the sepals (Plate   : 11) . The petal primordia further develop and become triangular, at which stage the stamen primordia appear (Plate   : 12) . The apparently imbricate petals enclose the stamen primordia (Plate   : 13) .

2.3.3   Differentiation of stamen primordia   The 10 stamens are arranged in 2 whorls of 5 (Plate   : 13) . In early May, five stamen primordia initiate simultaneously and alternate with the petals (Plate   : 12) followed by the remaining five stamen primordia, which are located between the stamens in the first row and differentiate simultaneously and opposite the petals . The stamen primordia rapidly develop into a globose structure (Plate   : 14) . When the 10 stamen primordia have become globose, initiation of the pistil primordia begins .

2.3.4   Differentiation of carpel primordia   In mid May, the apex of the flower primordia changes from dome shaped to flat . At the margin of the apex, five hemispherical pistil primordia initiate opposite the petals (Plate   : 14) . With the appearance of the pistils, the stamen primordia differentiate into filament and anther . The pistil primordia become conical and the apex of the pistil primordia becomes concave (Plate   : 15) . The five pistil primordia turn inward and move closer to each other and toward the center (Plate   : 16) . The development of the floral organs is identical in staminate and hermaphroditic flowers .

2.3.5   Transition from hermaphroditic to unisexual flowers   In late May, the five carpels primordia of hermaphroditic flowers turn inward (Plate   : 17) . The apex of each carpel primordium bulges and the bulges connect with each other (Plate   : 18) . The bulges then expand laterally more than in other directions . Later, the styles and stigmas (Plate   : 20) differentiate from connected-bulges of a pentagonal structure (Plate   : 19) . The styles, their base attached to each of the five ovaries, quickly elongate (Plate   : 21) . With the initiation of the style and stigma, the anthers and filaments become smaller and shorter .

In staminate flowers, however, the differentiation of floral organs differs from development in the hermaphroditic flowers . The five carpels turn inward and move close to each other, the same as in hermaphroditic flowers (Plate   : 22) , but then their development stops at the stage when the five carpels are connivent (Plate   : 23) . Neither the style nor stigma are differentiated . At maturity of the anthers, the five carpels, which are gradually surrounded by an external ridge

(Plate　: 24), degenerate (Plate　: 25, 26). In the staminate flowers, therefore, only stamens are observed and the carpels are difficult to see. The differentiation of the style and stigma in hermaphroditic flowers and the degeneration of the carpels in staminate flowers happens almost simultaneously.

In late May, most staminate flowers open, whereas flowering is delayed by several days in hermaphroditic flowers. Additionally, some aberrant flowers in which there are 6 petals, 12 stamens and 6 carpels in one flower are observed in both staminate and hermaphroditic flowers (Plate　: 27, 28).

3　Discussion

3.1　Differentiation of hermaphroditic and unisexual flowers

Our study shows that *A. altissima* is an androdioecious species with staminate and hermaphroditic individuals. The differentiation of floral organs in hermaphrodites is delayed about 4 or 5 days in comparison with staminate flowers. When petal primordia initiate in hermaphroditic flowers, the carpel primordia begin to differentiate in staminate flowers. The differentiation of floral organs is faster in staminate than in hermaphroditic flowers. Most staminate and hermaphroditic flowers open at the end of May. In hermaphroditic flowers, when carpel primordia begin to differentiate the style and stigma, the anthers are smaller and the erect filaments are shorter than the petals. In staminate flowers, we noticed that the anthers are larger and that the base of the filaments bend so that the anthers and filaments are wrapped by petals.

The development of the floral meristem in most hermaphroditic, staminate and/or pistillate plants is due to temporal and spatial regulation (Ma, 1994). After floral primordia form, they are able to generate sepal, petal, stamen and carpel primordia, respectively. Our observations of *A. altissima* also confirmed process. During floral development of *A. altissima*, the process of floral organ development is identical in both staminate and hermaphroditic flowers before initiation of the style and stigma, but the time of appearance of the floral organs differs. After initiation of the style and stigma, essential differences appear between hermaphroditic and staminate flowers. In hermaphroditic flow-

ers, the stamens and carpels differentiate normally, whereas in staminate flowers there is normal stamen differentiation, and abnormal gynoecium initiation. This phenomenon has also been observed in dioecious species of wild grape (*Vitis vinifera* ssp. *sylvestris*) (Caporali *et al* . 2003). The development of the floral organs in wild grape is divided into eight stages: the developmental pathways of staminate and pistillate flowers first begin to diverge at stage 6. In pistillate plants, the style and stigma differentiate normally, whereas they do not differentiate in staminate flowers. In the dioecious *Asparagus officinalis* sexual differentiation occurs later in the initiation of flora organs: in pistillate flowers, the stamens degenerate; whereas in staminate flowers, the ovary stops growing, but does not degenerate (Caporali *et al* . 1994).

3.2　Floral development and phylogenesis in androdioecy

The characteristics of floral organogenesis may play an important role in determining the origin and evolution of angiosperms and provide more important information about the relationship of plant species (Sun *et al* . 1998). Wolf (2001) indicates that androdioecy is a rare and unusual breeding system in which populations contain both staminate and hermaphroditic individuals. Although androdioecy is rare, its maintenance and evolution have broad implications for breeding systems.

Androdioecy is a rare phenomenon, but has been proven in *Datisca glomerata* (Presl .) Baill . (Liston *et al* . 1990). Durand and Durand (1992) inaccurately described sexual expression in *Mercurialis ambigua* L . (Euphorbiaceae) as andromonoecy, whereas it should have been referred to as hermaphroditic with both staminate and hermaphroditic flowers. Dioecy was suggested to be the ancestral state, and both monoecy and androdioecy were thought to be derived from dioecy in *Mercurialis* (Durand and Durand, 1992). Current phylogenetic analysis shows that dioecy has evolved repeatedly from androdioecy in the genus *Acer* (Gleiser and Verdú, 2005). Although androdioecy either evolved from hermaphroditism through the spread of a female-sterility mutation, or a dioecious state through the evolution of staminate function in females (Pannell, 2000). All of the clearest examples of androdioecy in-

dicate that it evolved from dioecy, because related species all have a dioecious sexual system (Pannell, 2002). Schneider *et al*. (2006) analyzed the family Quiinaceae using molecular phylogeny and found that bisexual flowers (*Froesia*) are ancestral in the family, whereas androdioecy (*Quiina*, *Touroulia*) and dioecy (*Lacunaria*) are derived breeding systems. Although there is no agreement on the evolution of androdioecy, many studies indicate that it may arise from dioecy and not from hermaphroditism.

3.3 Function of fertile structures in hermaphroditic and unisexual flowers

Most studies that have looked at examples of androdioecy have found evidence for cryptic dioecy in which the morphologically perfect flowers are functionally pistillate (Mayer and Charlesworth, 1991). Cao (2006) studied floral organogenesis and development of *Handeliodendron bodinieri* (Iévl.) Rehd. (Sapindaceae), the flowers of which are unisexual. In the pistillate flower, the ovary bulges and the stamens degenerate, whereas in the staminate flower, the stamens grow normally but the ovary degenerates.

In our observations, the *A. altissima* may be an androdioecious species morphologically and structurally, but it is difficult to explain the function of androdioecious species. Because most studies of the morphology of androdioecy have confirmed that androdioecious species are actually functionally dioecious, although pistillate plants are morphologically hermaphroditic (Charlesworth, 1984). Future studies may elucidate whether *A. altissima* is functionally androdioecious.

3.4 The molecular mechanisms of floral organogenesis

During the last decade, after the ABC model of genetic regulation of flower morphogenesis was put forward, substantial work has been devoted to locating and characterization genes controlling meristem and floral organ identity. There is a great variety, however, in floral architecture and organization within the plant kingdom and it is critical to ascertain the genetic mechanisms responsible for this variability by investigating a wider range of plant species (Baum *et al*. 2002). In *Atriplex halimus* L., day length and light intensity affect sex ratio and flower distribution and flower position on the reproductive axis, and the geographical origin of the plant (genotype) also affects sex and architecture ratios (Talamali *et al*. 2003). In *Rumex acetosa* L., a special stage of inappropriate arrested organ development is correlated with the closed expression of the C gene (Ainsworth *et al*. 1995). In cucumber (*Cucumis sativus*), sex is determined in unisexual flowers by the selective repression of growth or the abortion of either staminate or pistillate reproductive organs (Kater *et al*. 2001). The changes in organ identity in the expression patterns of B-function genes lead to sex determination occurring in *Asparagus officinalis* (Park *et al*. 2003). Interestingly, recently an AG-independent carpel development pathway was found in *Arabidopsis* (Pinyopich *et al*. 2003).

Androdioecy (mixtures of males and hermaphrodites) is a rare mating system in both the plant and animal kingdoms. Specific mechanisms of androdioecy have been most extensively examined in several species (Weeks *et al*. 2005). For example, in *Eulimnadia texana*, maleness is determined by a recessive allele at a single sex-determining locus (Sassaman and Weeks, 1993). Vassiliadis *et al*. (2000) reports that a gametophytic self-incompatibility system with links to nuclear sex determinism may explain the high frequency of males by causing frequency-dependent selection. Wolf (2001) examined the sex-determining mechanisms in the androdioecious species *Datisca glomerata* and its dioecious sister species *D. cannabina*, using a combination of traditional genetic crosses and molecular markers, and arrived at the following conclusions: (1) sex in both dioecious and androdioecious species of *Datisca* appears to be determined by a single nuclear locus, at which the male-determining allele is dominant; (2) the loci controlling sex determination in both species may be homologous; (3) hermaphroditism is recessive to femaleness and thus must have arisen as a recessive mutation restoring staminate fertility in females. Our observations confirm that *Ailanthus altissima* is morphologically androdioecious, but the mechanisms of formation of androdioecious plants need to be clarified in further research. Molecular and genetic studies of floral morphogenesis in species producing unisexual flowers remain scarce. The above cited studies report exclusively on rudimentary and aborted or-

gans . These studies clearly demonstrate, however, that plants that produce diversified floral phenotypes offer a unique opportunity for unraveling the genetic control of flower development, which is complementary to works on classical hermaphroditic model species . Research on the developmental genetics of floral organs and inflorescence morphogenesis plays an important role in the molecular mechanisms of the evolution of floral organs . *Ailanthus altissima* obviously produces unisexual and hermaphroditic flowers at inception . Its reproductive structures are highly plastic and amenable to environmental conditions, making it a unique and valuable subject for clarifying sex determination and development .

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Explanation of Plate

V . vegetative bud; L . compound leaf primordium; I . inflorescence primordium; B . bract primordium; a . apical meristem of shoot; LI . lateral inflorescence primordium; F . floral primordium; Se . sepal primordium; P . petal primordium; S . stamen primordium; C . carpel primordium

Plate : Floral organogenesis and development of *Ailanthus altissima* (Mill .) Swingle under scanning electron microscope

1 - 16 Inflorescence and floral organogenesis in staminate and hermaphrodite　1 . Apical meristem of vegetative buds; 2 . Differentiation of primordia of main inflorescence axes; 3 . Initiation of bract primordia; 4 . Finishing of primordial differentiation of main inflorescence axes and shoot apex; 5 . Initiation of lateral inflorescence axes primordia in axils of bracts; 6 . Development of primordia of lateral inflorescence axes; 7 . Mode of differentiation of primordia of lateral inflorescence axes; 8 . Apex of flower primordium and initiation of first sepal primordium; 9 . Initiation of second and third sepal primordia; 10 . End of fifth sepal primordium differentiation; 11 . Differentiation of petal primordia; 12 . Initiation of stamen primordia; 13 . Tegular petals encasing stamen primordia; 14 . Initiation of gynoecial primordia; 15 . Concave apex of gynoecial primordia; 16 . Development of carpel primordia . 17 - 21 . Development of gynoecial primordia in hermaphrodites　17 . Five carpel primordia close to each other; 18 . Initiation of stigma; 19 . Development of stigma; 20 . Initiation of pentagonal stigma and style; 21 . Connected carpels at base of style . 22 - 26 Development of gynoecial primordia in staminate flowers 22 - 23 . Five carpel primordia gradually becoming close to each other; 24 . Shrinking and diminishing five carpel primordia; 25 . Carpel primordia further degenerated; 26 . Carpel primordia absent at anther maturation; 27 . Six petals and twelve stamens in one flower; 28 . Six gynoecial primordia in one flower